Vol. VI. *January, 1904.* *No. 2*

BIOLOGICAL BULLETIN.

FORM-REGULATION IN CERIANTHUS, III.

The Initiation of Regeneration.

C. M. CHILD.

In the first paper of this series ('03*a*) the typical course of regeneration in a cylindrical piece was described; in the second paper ('03*b*) some of the factors influencing the process of regeneration as a whole were discussed; these papers have served to clear the ground for a detailed analytical study of the process of regeneration in *Cerianthus* in its various manifestations. In this and following papers of the series various phases of this subject will be considered.

Changes in Form Consequent upon Section.

The reduction in size of the opening at the end of a cut piece by the bending inward of the cut margins was described in its simplest form in the first paper of this series. A somewhat more general consideration of this peculiar process is necessary before proceeding to the discussion of other points.

Early in the course of my experiments upon *Cerianthus* it was noted that in nearly every case, however the pieces might be cut, the body-wall became rolled or folded in such a manner that the opening into the enteric cavity resulting from the cut was much reduced in size or was closed by approximation or contact between different parts of the body-wall. The usual result of the infolding is the complete removal of the entodermal surfaces from contact with the external water, *i. e.*, the piece rolls up or closes in such manner that the entoderm is on the inside. For convenience we may designate inrolling about a transverse axis as transverse inrolling, and inrolling about a longitudinal axis as longitudinal inrolling.

At first glance this process appears much like an adaptive reaction. In some cases it is almost as if the animal or part were

consciously closing the artificial openings. In the following paragraphs the principal forms of inrolling in the cut pieces are described.

The case of the closure of the ends of a cylindrical piece which was described in the first paper is the simplest of all. Collapse occurs with the escape of the water from the enteron and within

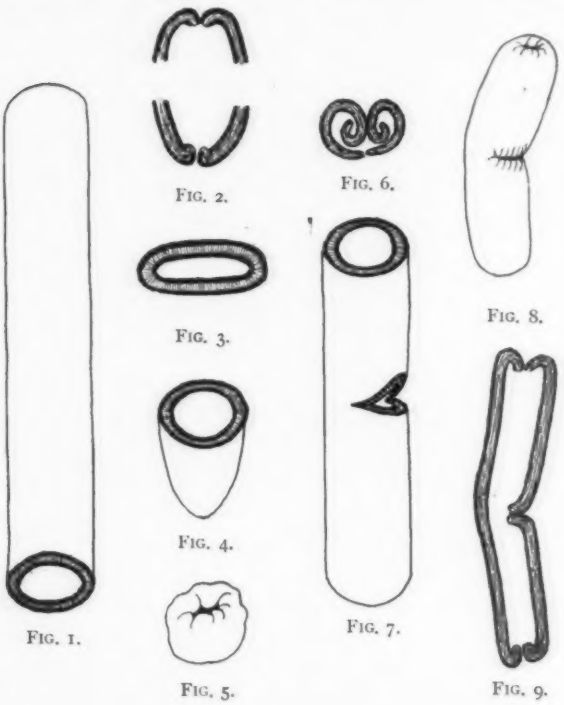

FIG. 1.

FIG. 2.

FIG. 3.

FIG. 4.

FIG. 5.

FIG. 6.

FIG. 7.

FIG. 8.

FIG. 9.

a few moments the cut ends begin to bend inward and finally close the openings except for the small slits between the folds. The diagrams, Figs. 1,[1] 2 and 3, illustrate this case, Fig. 1 representing the cylindrical piece at the time of section, Fig. 2 the longitudinal section of the ends after the bending in of the cut margins, and Fig. 3 a transverse section, indicating the flattening

[1] The diagrams representing the inrolling are much less highly magnified than preceding figures.

of the piece as it lies on a flat surface. In pieces of this kind complete collapse and contact of the body-walls is prevented by the large mass of mesenteries and mesenterial filaments which occupy the enteron. These are not represented in the figures, but they fill the whole enteron after collapse. Any solid mass in the enteron would of course have the same effect.

A piece cut from the extreme aboral end of the body (Fig. 4) differs in certain respects from the piece just described. Figs. 5 and 6 show the changes in a piece of this kind. Here the cut end becomes rolled inward to a much greater extent than in the previous case so that the enteron is nearly filled by the inrolled portion and the cut surface is so situated that closure by growth of new tissue from this surface is impossible. The reason for the greater degree of rolling in this piece as compared with the longer piece is undoubtedly to be found in the absence of mesenteries, except a single pair, in the aboral region. Since the enteric cavity is not filled with a mass of mesenterial filaments as in a region further orally the inrolling continues until the entire cavity is practically obliterated by the inrolled parts.

If a cut be made in one side of the body or a piece removed as in Fig. 7, the cut edges roll inward as in other cases, but in addition to this the body becomes bent at the level of the cut, so that here also the inrolled edges are brought into contact (Figs. 8 and 9).

The widest departures from the typical form are found, however, in those pieces which were cut longitudinally as well as transversely. In these the results differ to some extent according to the shape and relations of the pieces. Fig. 10 represents a cylindrical piece split longitudinally on one side. One form after collapse and inrolling of cut margins is shown in Fig. 11. Fig. 12 represents a transverse section and Fig. 13 a longitudinal section of one end. In Fig. 14 another form of closure is represented; here the ends fold over to a greater extent so that the opening is entirely on one side of the piece. Fig. 15 represents a transverse section of this piece and Fig. 16 a longitudinal section in the plane indicated by the vertical line in Fig. 14.

In most cases, however, the right and left longitudinal cut edges do not roll inward with equal rapidity and the result is

that the piece rolls up spirally on its longitudinal axis. Such a case is shown in Fig. 17; here the inner and outer coils of the spiral are on the same level at the outer end of the piece. Fig. 19 shows a spirally coiled piece in which the inner coils are higher than the outer. Figs. 18 and 20 represent longitudinal sections of one end of these pieces and Fig. 21 a transverse section.

The Figs. 11–21 represent only the chief types resulting from pieces like Fig. 10. All possible intermediate forms and modifi-

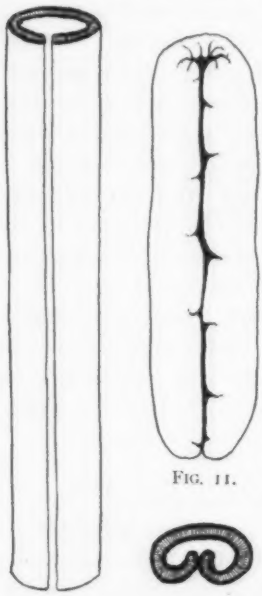

FIG. 10.

FIG. 11.

FIG. 12.

FIG. 13.

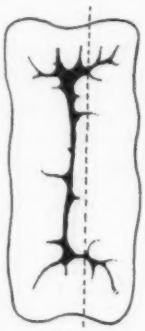

FIG. 14.

FIG. 15.

FIG. 16.

cations of these different types occur, the differences depending on various conditions, but chiefly on the relative rapidity of the inrolling in the different directions.

Semi-cylindrical pieces or longitudinal strips may roll either longitudinally or transversely. The greater the length and the less the breadth of the strip the more likely it is to roll transversely. Figs. 22–24 show a strip and two forms of transverse rolling which it may undergo. The longitudinal strips

often roll longitudinally soon after section, but by gradual inrolling of the ends finally become rolled transversely.

Loeb ('91) has suggested that the cut edges roll inward because the inner layers of the body-wall are stretched to a greater degree than the outer layers; this view assumes that all layers are more or less similar in elasticity and therefore that the layer that is most stretched will undergo the greatest contraction when the tension ceases. It is difficult to understand why one layer of the body should be more stretched than another, since all have been subjected to the same conditions, viz., the tension resulting from the fluid pressure on the walls of the enteron.

FIG. 17.

FIG. 18.

FIG. 19.

FIG. 20.

FIG. 21.

FIG. 22.

FIG. 23.

FIG. 24.

I am inclined to believe that this remarkable capacity for rolling which the pieces exhibit is due primarily to a difference in elasticity between the different layers of the body-wall, though it may be increased or modified by other factors. The succession of layers in the body-wall is as follows: ectoderm, longitudinal muscles, mesoglœa, entoderm. The mesoglœal layer is fibrillar in appearance and, while not as thick as the muscular layer, is well developed.

Judging from the fact that this layer is not folded or wrinkled, even in strongly contracted animals, the inference that it possesses

a considerable degree of elasticity appears justifiable. Under normal conditions the body-wall is subjected to tension. By section of the body at any point the internal pressure is removed and collapse occurs; the body-wall is no longer under tension and contraction of the elastic layer begins. If the ectoderm and muscles are to a large extent passive in this elastic contraction the result will be not simply a reduction in surface area, but an inrolling of the body-wall, since the mesoglœa is situated near its inner surface.

The fact that the region near the cut surface is always more strongly rolled than other parts may perhaps be the result of the direct injury to the tissues in this region, causing contraction, but here as elsewhere the contraction must be greater in the inner portions of the body-wall than in the outer, otherwise inrolling could not occur. More probably, however, the greater degree of inrolling near the cut surface is largely, if not wholly due to the fact that the physical obstacles to the inrolling offered by resistance of other tissues, etc., are much less near a free end or cut surface than elsewhere and the effect of elasticity is therefore greater. It appears probable from the preceding considerations that the mesoglœa plays the chief part in the inrolling about the cut surface as well as in regions distant from it.

Objection to this view may, however, be made on the ground that a tonic muscular contraction resulting from the injury is not only a possible but a much more probable cause of the inrolling. A brief consideration of the facts is sufficient to show that the inrolling cannot be explained as the result of muscular contraction.

This is evident first from the fact that it occurs in all directions, longitudinally and obliquely as well as transversely. If it were the result of muscular contraction we should expect it to occur only transversely since the body-wall contains only longitudinal muscles. It is difficult to understand how the contraction of longitudinal muscles could account for the inrolling of a longitudinal cut margin, since the muscle fibers are parallel to the cut. Moreover, there is no apparent reason why the inner portions of the muscular layer should contract more strongly than the outer, since all must be equally affected by the injury. And finally, observation renders it very evident that the inrolling is

not due to muscular contraction, for although strong contraction occurs at the time of section the muscles relax within a few moments and before inrolling begins. Moreover, the muscular contraction consequent upon stimulation of pieces after inrolling has occurred causes in most cases a more or less complete unrolling, provided the inrolling was in the transverse direction but does not affect inrolling in the longitudinal direction. In the light of these facts it is difficult to escape the conclusion that the inrolling is caused by some part of the body-wall axial to the muscular layer, viz., either entoderm or mesoglœa. The delicate cellular layer of entoderm cannot be supposed to possess any such elasticity; there remains therefore only the mesoglœa.

It now remains to consider whether the different forms of inrolling described and figured above are all explicable on the basis of elasticity of the mesoglœa. For this purpose we may regard the tension as resolved into longitudinal and transverse components.

As regards the inrolling of cylindrical pieces with transverse cut margins (cf. No. 1 of these studies, '03*a*, also Figs. 1 and 2 of the present paper), it is easy to see that it can proceed only a certain distance. Since the elastic tension is present in all parts of the cylindrical piece reduction in size may occur, but the cut ends are the only regions where marked change of form can take place. These are bent inward until the more prominent folds come into contact and the size of the opening is reduced. Beyond this the inrolling cannot go since contact between different parts of the margin and the radial folds into which the contracting margin is thrown both oppose further change. The appearance of the radial folds requires a word of explanation. Their presence would seem at first glance to indicate that elastic tension exists only in the longitudinal direction. A brief consideration will show, however, that this is not the case. After escape of the water from the enteron and collapse of the body, reduction of the circumference occurs throughout the whole piece, undoubtedly in consequence of the elasticity of the body-wall. There is, however, no physical ground for greater contraction in the transverse direction at the ends than elsewhere since there is no break in the transverse continuity of the body-

wall. The longitudinal component must cause inrolling at the cut end until either the local tension due to the formation of radial folds in consequence of the inrolling or the mutual contact of appressed portions of the inrolled wall opposes a resistance equal to the elastic tension. It is probable that in the oral half of the body, the mass of mesenteries and mesenterial filaments also oppose more or less resistance to the inrolling margins.

The flattening of the piece which often occurs (Fig. 3) is simply the result of gravity. If the collapsed piece lies on one side during several hours the weight of the body-wall is sufficient to bring about the flattening to a greater or less extent. In consequence of the flattening the openings at the ends are frequently elongated in the plane of flattening and slit-like, the inrolling occurring chiefly on the two margins of the slit.

In pieces from the extreme aboral end the inrolling at the cut margin may proceed much further (Figs. 4–6). Here the body-wall and especially the muscular layer is much thinner and must offer much less resistance to the elastic tension. Moreover, the enteron is practically empty in this part of the body. In consequence of these conditions the inrolling may proceed so far that portions of the margin are directed orally (Fig. 6).

The closure of a lateral cut by bending of the whole piece (Figs. 7–9) especially resembles a definite adaptive reaction, but can be explained as the result of elastic contraction. A cylindrical piece such as Fig. 1 does not become bent or curved so long as elastic tension on opposing sides of the body is equal. If in any way the tension on one side be reduced in effectiveness the body must bend toward that side. A transverse cut through the body-wall on one side, or the removal of a piece as in Fig. 7 interrupts the continuity of the body-wall. The longitudinal component of the elastic tension acts on the parts above and below the cut and causes contraction and inrolling of their edges. But by removal of a piece of the body-wall an open space is left and the longitudinal component of tension on the opposite side of the body causes bending of the piece so that the concave surface is on the side of the cut. The larger the piece cut out from the one side the greater will be the bending since it will continue until contact between the cut margins affords a resistance equal to the opposing tension.

Figs. 10–21 require little explanation. Here transverse continuity is interrupted by a longitudinal cut on one side. The form of the piece after inrolling is at least in large part a matter of chance, being dependent upon the relative rapidity with which the different margins roll inward.

In Fig. 11 the inrolling at the ends has been less than in Fig. 14 and the resulting form is different. In Figs. 17–21 the spiral form is due simply to the fact that one longitudinal cut margin rolled inward somewhat more rapidly than the other. An oblique spiral results from more rapid inrolling of the longitudinal margin near one end. It is clear that various conditions such as the degree of contraction of the muscles of a certain part of the body, the resistance offered by the mesenteries, the position of the piece in the aquarium, etc., may constitute conditions affecting the result.

The frequent rolling about a transverse axis of longitudinal strips cut from the body is clearly the result of the predominance of the longitudinal component of tension. It is interesting to note that this transverse rolling occurs only when the muscles are fully relaxed. If the piece be stimulated sufficiently to cause strong muscular contraction more or less complete unrolling often occurs. Pieces of this sort frequently roll about a longitudinal axis after cutting while the muscles are more or less contracted and then as the muscles relax after a longer or shorter time begin to roll transversely and continue until completely rolled up in a single or double spiral.

In cases of spiral or transverse inrolling (Figs. 17, 19, 23, 24) there is little resemblance to an adaptive reaction. As will appear, typical regeneration is impossible in these cases. Since it is scarcely to be supposed that in pieces of a certain form the reaction is adaptive in nature while in pieces of other forms it is due merely to elasticity it is preferable at least to attempt to analyze the apparently adaptive reaction. In the present case I think the analysis has demonstrated that the various methods of inrolling are all explicable on the basis of elastic contraction of the mesoglœa. The apparently adaptive character of the inrolling in cylindrical pieces where it results in more or less perfect closure of the ends is due to the particular physical conditions

present in such pieces. The inrolling of pieces after section is not then a definite reaction adapted to close the wound, except in so far as we may regard the presence of an elastic layer in the body-wall as an adaptation.

After the inrolling is completed gradual reduction in the size of the whole piece continues until the artificial openings are closed by new tissue or otherwise and the water pressure is again established in the enteron. This reduction in size can scarcely be due to the loss of tissue in the absence of food, for that is much less rapid. The piece appears to contract continuously after collapse and closure and if the closure and distention with water is prevented in any way, becomes much reduced within a few days. Frequently new wrinkles or folds appear as the contraction progresses, indicating that it is not due to actual loss of material but to some other cause.

There can be no doubt that this reduction in size of collapsed pieces is simply a continued reduction in the surface area of the tissues resulting from mechanical conditions. It is due at least in part to the elasticity of the body-wall (or especially of the mesoglœa). This being effective in all directions must cause gradual reduction in size of the whole after the inrolling of the margins is completed, unless it is counterbalanced in some way, which is not usually the case. This quality of the body-wall is remarkable; pieces kept under conditions where distention with water is impossible often contract to half the size after section and collapse. If they are then permitted to close and become distended with water they may again attain in two to three days almost the original size, provided the period during which they remained contracted was not too long. The longer the period of collapse the slower and less complete is the return to the original size. These facts indicate that in the absence of the tension due to internal water-pressure the tissues gradually rearrange themselves in accordance with the altered physical conditions. There is no return to the "normal" form unless mechanical conditions once more become normal.

In his study of *Cerianthus*, Loeb ('91) has attempted to explain the collapse of tentacles and other phenomena by loss of turgor in the cells. As I shall show in a later paper, this explanation is

wholly incorrect. The question as to whether osmotic phenomena play a part in the changes above described requires, however, a moment's consideration. As regards the inrolling after section and the reduction in size of the collapsed pieces there is certainly no reason for supposing that it is due to changed osmotic conditions. It is difficult to understand how, in a form like *Cerianthus* section of the body-wall at one level should cause changes in turgor in the cells of the whole piece or of those at a distant region unless we suppose that special stimuli producing these changes arise from the region of the cut. If this be the case then the change is not primarily osmotic but reactive. Moreover, the phenomena are so obviously due to elasticity that the search for any other explanation is clearly unnecessary.

The Rôle of the Slime Secretion in the Closure of the Enteric Cavity After Section.

As has been shown, the inrolling of the margins of the piece under ordinary conditions approximates the various parts of the cut surface, and thus reduces the size of the opening. The radiating wrinkles and folds into which the inrolling portions are thrown and the frequent protrusion of parts of the mesenteries through the opening render the closure by contact imperfect. There are always slits and angles between the various parts, through which the enteric cavity is in communication with the exterior.

In spite of this fact I have often found pieces distended with water, before any closure of the ends by new tissue has occurred. A series of experiments in which the body-wall was sectioned transversely at some level and the oral portion, still bearing tentacles and disc intact, was used, will serve to illustrate this point. In every case collapse of the tentacles and body occurred immediately after section, owing to the escape of water from the enteron, but very frequently the whole oral piece including the tentacles was again distended with water in less than an hour. Examination of the aboral cut end in such cases showed that inrolling and approximation of the margins had occurred, but frequently distinct spaces between the wrinkles could be observed opening into the enteron. If the end were spread open with

needles collapse occurred at once, but was followed by renewed extension in a short time. Pieces with tentacles and disc intact show these changes much better than others, since the phenomena of distention and collapse are especially conspicuous in the tentacles. Moreover, in these pieces the presence of the mouth permits much more rapid entrance of water than is possible in pieces with oral end removed, since in these latter there is no apparatus for forcing the water into the enteron. The rapid distention of pieces under the conditions described is made possible only by the ectodermal slime secretion which under normal conditions forms the tube.

The manipulation incidental to section of the body and the stimulus of the cut itself cause a rapid secretion of this slime during the operation and for some time after. The secretion is tenacious even when first formed and clings closely to the body.

After inrolling has occurred at a cut surface only ectoderm is visible from without and where different parts of the inrolled margins are in contact the contact is usually in part ectodermal. The slime is secreted over this inrolled portion and forms a tenacious coating which closes all the crevices between the inrolled portions of the body-wall. Thus, so far as the escape o water in appreciable quantities is concerned, the cut end may be closed within a short time after section, almost as soon, in fact, as the inrolling is completed.

If the piece is left undisturbed the slime accumulates and the closure becomes more and more complete until finally the thin membrane of new tissue constitutes the definitive closure. If at any time before the definitive closure the slime be carefully removed with needles without causing violent contraction or changes in form of the piece, collapse will occur at once, showing clearly that the slime alone prevented the escape of the water.

The Growth of New Tissue from the Cut Surface.

The closure of the ends by new tissue was briefly described in the first paper of the present series, but the conditions which determine it were not discussed.

As described, the course of the process at both oral and aboral ends in typical regeneration is as follows: First the appearance of

a thin membrane of new tissue between those regions of the cut surface which are sufficiently approximated; the growth of this membrane until the whole opening is closed; the increase in size of the area of new tissue as the piece becomes distended.

During the course of my experiments it was found that certain definite conditions are necessary for this growth of new tissue.

Mention was made of the fact that the new tissue appears first in the folds and wrinkles where two cut surfaces are most closely in contact and that from these regions it extends until closure is complete. In pieces rolled spirally (Figs. 17, 19, 24) or in any such manner that the cut surfaces are not brought into contact no appreciable growth of new tissue occurs; the cut edges heal, but may remain without further change for months.

Thus, in these spirally or transversely rolled pieces typical regeneration of new tissue from the cut surface does not occur. Moreover, this is true of all cases in which there is no approximation or contact of two cut surfaces or parts of a cut surface. Never is a thin membrane of new tissue found growing out from a cut surface and without other connections. When present it always connects two cut surfaces or the two sides of a fold where different regions of the cut surface have been approximated.

This is a point of considerable importance; indicating as it does that there is nothing in the cut surface itself which initiates regeneration, the necessary condition being found rather in the relations of different cut surfaces or their parts. *Never* do we find regeneration of the body-wall occurring in the manner represented in the diagram, Fig. 25, as a continuation with free margin of the old tissue. New tissue arising from cut surfaces always appears between two cut surfaces which are in contact or closely approximated as in Fig. 2. These surfaces become united by new tissue which then increases in amount under certain conditions, thus forming a thin membrane connecting the two parts of the cut surface. In the ordinary closure of the end of a cylindrical piece the new tissue first appears, as has been noted, in the folds and wrinkles where parts of the cut surface are closely approximated (Figs. 6–8, '03*a*), but from this it spreads rapidly until the whole space is covered and the end closed (Fig. 9, '03*a*).

The process is briefly as follows: After exposure of a cut surface some slight proliferation occurs which results in healing unless another cut surface be so near that the cells arising from both are in contact; if this is the case then organic union between the two cut surfaces is rapidly established. In the closure of the ends of cylindrical pieces this process is usually completed in a few days, but in certain other cases it may proceed much more slowly. For example, in pieces which are split down one side (Fig. 10) and in which both of the longitudinal cut margins roll inward as in Fig. 11, the process of closure often requires two months or more for completion. In such cases the longitudinal cut margins usually roll inward so far that they are not in contact. At one or both of the ends, however, the closure may occur in nearly the typical manner. From the end the new tissue begins to grow along the longitudinal cut, and as it grows actually draws the cut edges together to a certain extent. The process may be compared for the sake of illustration to that of sewing up the longitudinal slit in the piece from one or both ends. If we take, for example, a case where two cut surfaces are in contact at one point and diverge at an acute angle from this point, we find that the growth of new tissue always begins at the point of contact. From this point growth and the formation of a thin membrane continue for a certain distance along the diverging cut surfaces, the extent of the membrane depending in a given species on the angle of divergence of the surfaces. This thin membrane is itself somewhat elastic and so tends to approximate the cut surfaces in greater or less degree unless opposed by other conditions. The approximation of the surfaces renders possible a further extension of the membrane between them, and so the process continues unless at some point the cut surfaces are so situated that the elasticity of the new tissues is insufficient to bring them into contact, or near enough to permit the extension of the thin membrane between them. In such a case the process of closure must cease, as often occurs. That this is actually what occurs I have convinced myself by repeated examination of specimens cut in such manner that at least some parts of the cut surfaces were not in contact while others were. The diagrammatic Figs. 26–30 will serve to illustrate the process. Fig. 26 shows

a cylindrical piece slit down one side and represented as cut across obliquely to show the separation of the cut surfaces; the cut surfaces have rolled inward and the oblique section at the lower end of the figure shows that the inrolling along the longitudinal cut is so great that the cut surfaces are not in contact. The growth of new tissue and closure begins at the oral end (it may begin at the aboral end also) where the cut surfaces are much more closely approximated and the numerous folds afford

FIG. 25.

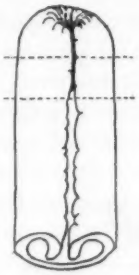

FIG. 27.

FIG. 30.

FIG. 26.

FIG. 28.

FIG. 29.

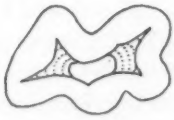

FIG. 31.

various points of contact. From this region it gradually extends along the longitudinal cut, drawing the cut surfaces together as it proceeds, as is shown by the two transverse sections, Figs. 28 and 29, Fig. 28 from a level where union has already occurred (the upper transverse line in Fig. 27) and Fig. 29 from a level just beyond where the cut surfaces have united (the level of the lower transverse line in Fig. 27). In Fig. 28 the margins have been drawn together and united, in Fig. 29 they are not yet in contact but are nearer together than at the level of the oblique section at the lower end of Fig. 27. In Fig. 30 the closure is

finally complete. In these figures only one end has been shown; usually, however, closure proceeds from both ends, and the middle portions are the last to become united.

It is evident that in a spirally or transversely rolled piece this process can never occur, for even if it begins in some fold or local approximation of the cut surfaces it cannot continue, because approximation of the cut surfaces to a degree sufficient to permit their union by new tissue is impossible as long as the piece remains spirally or transversely rolled.

Description of all possible cases of closure of pieces cannot of course be attempted. Results depend so largely on chance, that every piece affords, it might almost be said, a different solution of the problem. The examination of hundreds of pieces has, however, convinced me that the essential features of the process are those described above.

The cut surfaces appear to remain capable of giving rise to new tissue for an indefinite period. Often closure of pieces slit open longitudinally is completed only two or three months after section; yet during all this time the cut surface retains the power of producing new tissue under proper conditions, though it has no power to produce anything more than the proliferation connected with healing, provided it is not in contact with another surface. Union is as complete and perfect, though perhaps not as rapid, when it occurs two months or more after section as when it occurs within a few days.

When we compare *C. solitarius* and *C. membranaceus* we find that in the latter species the thin membranous growth of new tissue if once begun between cut edges in contact, may continue until it forms a connecting membrane between widely separated cut surfaces; in *C. solitarius*, on the other hand, the membrane is incapable of bridging over spaces so wide; the new tissue ceases to extend long before a point is reached where the cut surfaces are so widely separated. This difference is so marked that it raises the question as to whether there is a fundamental difference in the conditions and method of growth of new tissue in the two species. Figs. 6–9 of paper I. ('03*a*) and Fig. 31 of the present paper (an aboral end) illustrate the closure of openings in *C. membranaceus*. In Fig. 31 the new tissue which is

growing over the opening is in two parts which are advancing to meet near the middle. The concave free margin of both portions is noticeable. The dotted lines represent various stages in the growth of the new tissue. It is evident that it appeared first in the angles where two cut surfaces were in contact or very closely approximated. In *C. solitarius* closure by new tissue of only very much smaller pieces is possible. I believe the explanation of this difference is to be found in the different quality of the thin membrane of new tissue in the two cases. In *C. membranaceus* it is much thicker, more resistant, and less easily ruptured than in *C. solitarius*. The new tissue arises at a region where the cut surfaces are close together and may extend from this to regions where they are more widely separated. As was shown above, it exerts a certain degree of tension on the parts connected by it. As the distance between the cut surfaces increases a point may finally be reached where the tension is equal to the cohesive power of the tissue elements. Beyond this the new tissue cannot extend. In *C. solitarius* this limit is attained with a slight separation of the cut surfaces, while in *C. membranaceus* the new tissue is capable of resisting much greater tension and so of extending over wider spaces.

The membrane extending between the two cut surfaces may be compared with a fluid film bounded by lines diverging at an acute angle. The film extends a certain distance from the apex of the angle, this distance being determined with a given fluid by the size of the angle. The free margin of the film is always concave toward the opening of the angle. So long as the relation between cohesion and adhesion remains the same and the angle does not change the film can never extend beyond a certain point, since the surface-tension will cause rupture. As the angle and surface-tension decrease or as the adhesion increases the film will spread. If the arms of the angle are sufficiently pliable or capable of movement they may be drawn together by the surface-tension of the fluid, and thus permit further extension of the film.

In *Cerianthus* the thin membrane of new tissue which may be compared to the fluid film, arises at the apex of the angle, *i. e.*, where the two cut surfaces are in contact. The membrane extends along the diverging surfaces to a certain point. Its free margin is always concave (Fig. 31, also Figs. 6–8; '03*a*). The

distance to which the membrane spreads between the surfaces depends upon its composition and the degree of divergence of the surfaces, just as in the case of the fluid film. The thicker membrane with greater resistance will grow farther just as the film with less surface-tension will spread farther, other things being equal. Even the elasticity of the newly formed membrane is paralleled by the tension to which the fluid film is subjected. In both cases the margins of the space may be approximated by this tension and thus permit further spreading of the connecting film or membrane.

The illustration of the fluid film has been employed primarily as an analogy. It is not to be supposed that the thin membrane growing between two cut surfaces behaves in all respects like a fluid film extending across an angle. Yet the close parallelism between the two series of phenomena must raise the question as to whether after all the growth of new tissue from a cut surface in *Cerianthus* may not be, at least to a large extent if not entirely, determined by the laws which govern the behavior of fluids. The following facts point toward this conclusion: except so far as healing of a cut surface is concerned new tissue arises from a cut surface only when it is in contact with another, the thin membrane of new tissue which is under tension spreads between diverging cut surfaces to a certain point, beyond which no growth occurs, unless the surfaces are brought nearer together; the point where growth ceases differs in different species, depending on the quality of the membrane; the cut surfaces may themselves be approximated by the tension of the membrane and so further growth of the membrane made possible; the free margin of the membrane is always concave in the direction of growth, *i. e.*, the margins of the membrane extend further than its middle region. In all of these respects the thin membrane and the fluid film behave similarly. The conclusion is at least probable that the similarity in behavior is due to the fact that similar conditions are present. I think it probable, therefore, that the appearance and growth of new tissue from the cut surfaces of the body of *Cerianthus* is governed, at least to a large extent, by the laws of capillarity. Of course the cellular structure of the tissue may complicate conditions, and the thickening and structural differentiation which

occur in the membrane after its formation bring into play other factors. These need not be considered here, however. Certainly the phenomena are far from being adaptive or teleological in any sense although the closure of the cut might appear at first glance to be an adaptation. It is difficult at present to see how they can be due to anything except simple physical conditions, though it is possible that increased knowledge may afford another explanation. Provisionally then we may regard the delicate thin membrane which appears in the angles between cut surfaces as possessing some of the properties of a fluid and as subject, at least in large degree, to the laws of capillarity.

Whether these suggestions are correct or not, the two facts above mentioned are of great importance, viz., that regeneration of new tissue from cut surfaces occurs only when two surfaces are in contact, and that the new tissue cannot extend indefinitely between diverging cut surfaces but ceases at a certain point determined by the angle of divergence of the two surfaces and the (physical) quality of the membrane, *i. e.*, is different in different species. The only possible inference from these facts is that all conditions for regeneration are not given in the living tissues themselves, nor in these plus the normal environment as a whole, but that the formation of new tissue from a cut surface is probably dependent upon certain simple physical conditions similar to those which govern the existence of a liquid film between two diverging boundaries.

Healing of the cut surface does not require these conditions; for this the necessary conditions, which are very probably also primarily due to capillarity, are established by the cut itself. The same conditions are not, however, adequate for the formation of a membrane of new tissue from the cut surface.

In this case then the conditions for new growth and closure of a wound are to be found, not in the absence of a certain part, nor in the presence of a special stimulus at the cut surface, but in simple, external, physical relations of parts. Discussion of the bearing of these facts may be postponed to another time. Attention may be called, however, to the difficulty of reconciling these facts with the neo-vitalistic theories of life and especially with that of Driesch which is based upon the phenomena of form-regula-

tion and has adopted a modification of the Aristotelian idea of an entelechy as the basis of organic form.

Summary.

1. The inrolling of the margins and the closure of openings by contact of the inrolled margins is the result of the elasticity of the body-wall. This elasticity must be greater in the inner portions than in the outer portions, in order to produce the results observed. The facts indicate that the mesoglœa plays the most important part in this elastic contraction.

2. Openings between folds of the inrolled body-wall may be stopped by the ectodermal slime secretion. This method of closure often occurs in pieces before the formation of new tissue and permits the existence of considerable water-pressure in the enteron.

3. Contact or close approximation between two cut surfaces or parts of a cut surface is a necessary condition of the growth of new tissue from these surfaces. A single exposed cut surface may heal over but no further growth occurs from it.

4. The new tissue having arisen at a point of contact between two cut surfaces is capable of extending in the form of a thin membrane for a certain distance between diverging cut surfaces; the distance to which it extends is determined in a given species by the angle of divergence of the cut surfaces, and in different species by the thickness and quality of the membrane.

5. The new tissue rising between two cut surfaces behaves in certain respects as if subject to the laws of capillarity.

Hull Zoölogical Laboratory,
University of Chicago, September, 1903.

Bibliography.

Child, C. M.

'03a Form-Regulation in Cerianthus, I. The Typical Course of Regeneration. Biol. Bull., Vol. V., No. 5, 1903.

'03b Form-Regulation in Cerianthus, II. The Influence of Position, Size and other Factors upon Regeneration. Biol. Bull., Vol. V., No. 6; Vol. VI., No. 1, 1903.

Loeb, J.

'91 Untersuchungen zur physiologischen Morphologie, I. Heteromorphose. Würzburg, 1891.

AN ABERRANT LIMB IN A CRAY-FISH.

E. A. ANDREWS.

A striking aberration in the form of a third, left-walking leg of a female *Cambarus Bartoni* found in class dissection in February, 1892, seems of enough interest to warrant its being put on record.

A view of the anterior face of the limb (Fig. 1) shows a markedly forceps-like structure in addition to the usual forceps at the end of the limb, so that there are four instead of the usual two terminal points.

The added structure is, however, not a true forceps with one movable finger, but a movable piece with two immobile prongs

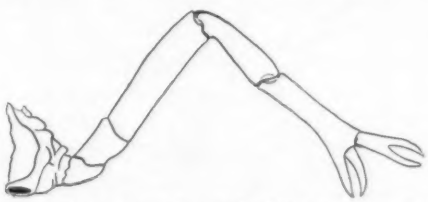

FIG. 1. Camera sketch of anterior face of left third leg of *C. Bartoni*. Genita opening indicated in black.

that otherwise resemble the index and pollex of a forceps. This is evident in the enlarged view, Fig. 2.

The real forceps in this limb is nearly normal, but on comparing it with an anterior view of the third walking leg of a normal *C. Bartoni* (Fig. 3), of about the same size, we may note some differences. Thus, in place of the straight-lined articulation of dactyl and propodite, we find the propodite presenting a hollowed, socket-like face where the dactyl articulates. Again, while the dactyl and the index are both normal in form, the dactyl is not a straight continuation of the propodite, but bends down at a noticeable angle, thus increasing the wide divergence of the double set of tips of this limb.

The propodite departs from the usual form in being wider distally where it bears, as it were, a large protuberance that is

truncated to articulate with the unusual pronged structure or second claw-like ending of the limb. There is also an abnormality in the propodite, indicated in Fig. 2, and suggesting some former injury; it is a slight indentation upon the middle of the anterior face.

The movements possible to the dactyl in the normal, alcoholic specimen (Fig. 3) are a swinging of 4.11 mm. in one plane to

FIG. 2. Anterior view of terminal part of Fig. 1. Camera. Zeiss 2, a.

bring about direct apposition of the tips of the forceps, with no overlapping and also a very slight lateral movement.

In the aberrant limb the dactyl is so set that apposition is imperfect; the dactyl passes the tip of the index by about .5 mm. while the entire swing is the same as above, 4.11 mm. The actual gape of the forceps is restricted to that same amount, .5 mm. All movement in this forceps is strictly in one plane.

Next considering the monstrous, pronged structure we find that, starting from the position shown in Fig. 2, there is a possible

movement of 2.5 mm. in the plane of the real forceps, one half of this being towards the forceps and one half away from it. There is also mobility at right angles to the above plane, in a general antero-posterior direction. Anteriorly this is 1.5 mm. and posteriorly about .7 mm., a total swing of 2.2 mm. On moving the abnormal structure and the normal dactyl as far as possible toward one another they came just into contact. The angle of divergence between the index and the most remote part of the abnormal structure is greater than the extreme opening of a normal claw.

The form of the pronged structure is remarkable for its symmetry: the two prongs (Fig. 2) differ but slightly in shape and in size. But the one standing nearer to the claw is slightly

FIG. 3. Camera sketch of an anterior view of a terminal part of the third left leg of a normal *C. Bartoni*.

thicker and less sharply pointed and it also lacks the clear, perforated horn-like tip present upon the other prongs as upon normal claws. That this tip was lost by wear or by accident seems evident from the rough surface ending the prong and from the fact that staining liquids easily enter at this point.

Since the anterior and posterior faces of the prongs are not alike one could not put either prong into a space of the shape of the other prong; the two prongs are symmetrical about a plane between them; they are mirror images of one another, except for the above noted difference in form. This symmetry extends to such details as the distribution of clusters of bristles or hairs and to the arrangement and number of the serrations along the opposed faces of the prongs.

This latter detail deserves special description. These serrations are like those along the opposed faces of the dactyl and the index and they add greatly to the *impression that the pronged structure*

is in some sort an imitation claw. On both dactyl and index is a long series of transverse plates closely crowded together and freely projecting to give the serrated appearance noticeable under a low power. Each plate is itself serrated near its tip but these fine serrations are seen only with a higher power. As these plates stand nearer to the posterior than to the anterior face of the claw, they are more readily seen from a posterior view. Each plate, like these in Fig. 4, stands obliquely transverse and is shaped like a scalene triangle with bluntly rounded apex. It is just below this apex that the outer and distal edge bears a series of sharp teeth. This fine serration is on the edge that faces posteriorly as well as distally and the plates overlap one another so that the teeth could not be seen from an anterior view, such as Fig. 2, were it not that the plates are so transparent that the teeth can be seen through the next overlapping plate. Each plate has a central canal that passes from the epidermis through the length of the plate and ends at the surface in the blunt apex: it passes by the serrations without any connection with them. Morphologically these plates seem to be flattened setæ or hairs. In this claw there are 61 plates on the dactyl and 67 on the index; three or four are broken. As seen in Fig. 2 the series of plates is longer on the index where the proximal six or seven plates are opposed by a bare space upon the dactyl. With this exception the plates of the index and dactyl correspond, each plate having its duplicate in the opposite series.

In the pronged structure there are two series of serrations showing this same symmetry; some of each series are represented in Fig. 4.

To save space the two series are drawn as if close together while in reality the rigid prongs always held the two series far apart (Fig. 2). The plate marked T is about the thirty-fifth one from the tip of the prong that has a perfect terminal spine. The edges with teeth are those nearer to the tip and also those farthest away from the serrations of the opposite series.[1] The edge turned toward the plate of the opposite series is smooth and free. The third edge of the triangular plate is the line of attachment and is

[1] The use of these serrated plates may be to aid in cleaning the animal rather than to aid in preparing food by acting against the opposed series; they may be like the combs on the legs of certain birds.

somewhat anterior to the free tip of the plate. The terminal plates are smaller than the others and have a smaller number of teeth. This number may be as high as twelve toward the middle of the series. In all these respects the plates of the monstrous growth agree with those of the real claw. No difference was found between single plates of the dactyl and the index, nor between plates of the two prongs nor between plates of the normal and abnormal growths.

The pronged structure, however, differs from the natural claw both in number of plates and in their arrangement at the angle. While the normal claw has 61 and 67 plates the pronged struc-

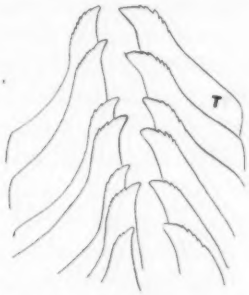

FIG. 4. Camera sketch of posterior view of serrated plates from the abnormal pronged structure. 2-D.

ture has 53 on the prong with a broken tip and 54 on the other. At the angle (Fig. 2) the plates have the arrangement shown in Fig. 5: the terminal plates are crowded together and the two series interfere at the angle. Plate 52 of the imperfect prong steps out of rank and stands partly in between plates 53 and 54 of the series on the perfect prong, which is indicated by the letter T on the fifty-second plate. The angle thus has plates of both series carried into it till they fuse into one curved line. Moreover, these plates at the angle are not the same as the terminal plates of the normal claw, nor do they agree in number of teeth with plates at that distance from the tip of the normal claw. They are evidently special terminal plates in their own series but not directly comparable with the normal terminal plates. The prongs are shorter than the index and the dactyl and have not room for a full number of plates. Where they have a free edge

it is set with plates at the same rate as on an equal length of claw edge. If the common base of the prongs were to be split for about two fifths of its length and the prongs so lengthened they could bear about seventy plates each and the prongs would be much more like the normal claw; still it would be necessary to transform the present terminal plates at the angle into plates of the right character in the new series and to make new terminals at the new proximal ends.

But little was made out regarding the internal anatomy of this abnormal limb either from preparations cleared and stained or from sections; but it was evident that the muscles in the propo-

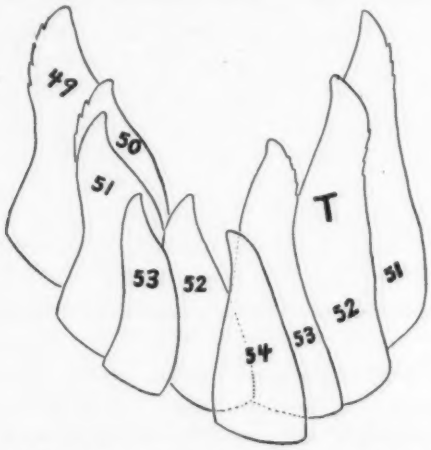

FIG. 5. Camera sketch, 2-D, of a posterior view of the plates at the angle between the two prongs.

dite were not arranged as in a normal propodite. At the distal end there were two muscle masses that seemed to connect with opposite edges of the articular end of the pronged structure. These would probably move this structure up and down in the plane of the claw. The usual muscles of abduction and adduction seemed to be developed, but attached to the dactyl in an abnormal way in connection with the above extra muscles and with abnormal widening of the distal part of the propodite.

The gist of the above description is that this abnormality is a case in which the propodite is to some extent double and bears a

normal claw as well as a pronged structure that simulates a claw even in details and was probably movable after the manner of a dactyl. This pronged structure is remarkable for its symmetry.

Comparing this with other described cases we find in the first place that it is unusual in being upon a walking leg. Of the thirty-one cases of abnormal appendages quoted by Bateson,[1] two are of antennæ, four are of non-chelate legs, and all the rest of chelæ except one, which is of a chelate walking leg.

Of the eleven additional cases given by Herrick[2] only two are of walking legs. However, this relative infrequency of described abnormalities in walking legs may be due, in part, to the greater ease with which other cases are collected or noted.

In the second place, it is unusual in being a monstrosity of the propodite. Bateson found the greater number of cases of repetition of parts, in the Crustacea, are repetitions of extra dactyls upon a normal dactylopodite (some fifty cases), and that next in frequency are the cases of extra index upon a normal index (some fifteen cases).

In the third place it seems to fall into none of the four categories established by Bateson, but rather to be like the exceptions, of which he found only two.

It has, however, resemblance to the case 815 of Bateson and more to the case shown in Fig. 195 of Herrick and still more to the case shown in Fig. 2 of Faxon,[3] which was described as follows: "This leg is provided with two chelæ. One of them has the ordinary form and structure, but is bent at a strong angle with the long axis of the leg. The second appears to have been budded off from an amputated surface of the propodite. It consists of two fingers which have the form of the normal dactylus and index, but neither is articulated with the other at the base. The two fingers together seem to be morphologically equivalent to a single segment, and represent a two-branched supernumerary dactylus."

Though the pronged structure we have described is markedly like a claw in its symmetry yet any tentative attempt to interpret

[1] Bateson, "Materials for the Study of Variation," 1894.

[2] Herrick, "The American Lobster," *Bull. U. S. F. C.*, 1895.

[3] Faxon, "On Some Crustacean Deformities," *Bull. M. C. Z.*, VIII., 1880.

it morphologically would seem to meet with more difficulty in assuming it to represent a claw than in assuming it to represent two fused dactyls or a branched dactyl. Were it a claw with fused articulation of dactyl and index we would have a limb so doubled distally as to have an extra segment and a lack of coincidence between the two series of segments. A propodite would spring from propodite instead of from a carpodite; and if we bear in mind the partial double appearance of the propodite and regard it as a fusion we would have a carpodite and a propodite springing from a carpodite, and so on.

Bateson's thorough study led to the conclusion that almost all cases could be interpreted as repetitions of claws in which there was more or less suppression of index or of carpus. The pronged structure would then be regarded as two party fused dactyls placed face to face and we would expect to find some representative of the two indices. On the line of imagined fusion there is a slight eversion of membrane where the pronged structure articulates with the propodite, but there is no reason for regarding this as of any morphological significance.

In the case described by Faxon, as quoted above, Bateson thought he had found a representative of the required indices in a small protuberance shown in Faxon's Fig. 2; this however was an error for I am informed by Faxon that "the artist unfortunately represented a protuberance which does not exist."

There are thus two cases in which pronged structures have nothing with them to countenance the idea that they represent double dactyls with even traces of double indices. Moreover, it will be seen from the above Fig. 2 that the prong nearer to the dactyl is not a mirror image of that dactyl but that it represents the index and likewise the other prong is not a mirror image of the index but represents the dactyl; this is true since all have their serrations nearer to the posterior face than to the anterior face. There is thus a departure from Bateson's rule of symmetry and we have to deal with a very unusual abnormality that is not interpretable in the same way as most of those hitherto known.

But any morphological interpretation seems somewhat premature and unsatisfactory in the lack of more knowledge of the

mode of formation of such structures. The appearance of the limb suggests a new growth following some injury in which the material for claw making was partly severed and displaced. This might happen, we can suppose, not only in the egg and in the young, but in the adult, especially at the periods of shedding when the interior of the claw is soft and the blood peculiar. That limbs may regenerate from a peripheral wound was shown by Herrick for the tips of the claws and by Morgan[1] for large parts of the limb. Possibly then such a monstrosity as this might arise in regeneration following an injury to the propodite.

An attempt to get experimental evidence resulted in failure, but this is what would be expected from the rarity of such monstrosities and from the difficulties in keeping the material long enough. In that attempt 103 mature *Cambarus affinis* were operated on in February. In each a deep cut was made in the carpodite of each chelate walking leg at a point corresponding to the pronged structure in this abnormal limb. In ten days many had healed, some could again use the dactyl and some had dropped the parts peripheral to the cut. Subsequently a piece was removed where the cut had been made in order to prevent such rapid healing. The breeding season then came on and after some months all the specimens had died without shedding and no new formations were found.

[1] Morgan, "Regeneration of the Appendages of the Hermit Crab and Crayfish," *Anat. Anz.*, XX., 1902.

THE REACTION-TIME OF GONIONEMUS MURBACHII TO ELECTRIC AND PHOTIC STIMULI.[1]

ROBERT M. YERKES.

CONTENTS.

PAGE.
Problems and Methods 84
Reaction-Time to Electric Stimuli 85
Reaction-Time to Photic Stimuli 86
Relation of Reaction-Time to Region Stimulated 88
Reaction-Time of Tentacles 89
Relation of Quality of Stimulus to Time of Reaction 91
Absolute and Relative Variability 92

PROBLEMS AND METHODS.

The reaction-time method as applied to the study of the functioning of the nervous system has already given us certain important facts in human neuro-physiology, and it promises much more valuable results when its application to representatives of the various animal phyla makes a comparative survey of the time relations of neural processes possible. The value of reaction-time studies lies chiefly in the knowledge which they give us of the biological significance of the nervous system. "Certainly they are not important as giving us knowledge of the time of perception, cognition or association, except in so far as we discover the relations of these processes, and the conditions which are most favorable for them. To determine how this or that factor in the environment influences the activities of the nervous system, and in what way system may be adjusted to system or part process to whole is the task of the reaction-time investigator."[2]

For the reaction-time measurements which furnish the material of this paper chronoscopic methods were employed. All reactions to light were measured by means of a stop watch readable to tenths of a second, but for the reactions to electric stimuli, which were very much quicker, it was necessary to make use of

[1] From the Marine Biological Laboratory, Woods Holl, Mass.

[2] Yerkes, Robert Mearns: "The Instincts, Habits and Reactions of the Frog." *Harvard Psychological Studies*, Vol. I., 1903, p. 509 (*Psychological Review Monograph Supplement*, Vol. IV.).

an instrument readable to hundredths or thousandths of a second. For this purpose a Hipp chronoscope, readable to thousandths, was placed in circuit with the stimulus electrodes and the reaction-key. The electrodes were connected in such a way that the chronoscope circuit was made, and the record thereby started, the instant the stimulus circuit was completed. The motor reaction of the medusa in response to the electric shock served to break the chronoscope circuit, thus stopping the record. The experimenter was then able to read from the chronoscope dials the time which intervened between stimulus and reaction (reaction-time). Cattell's falling screen served as a regulator for the chronoscope.[1]

The reaction-key used in these measurements of the time of reaction to electric stimuli consisted of a frame for the support of an easily sliding rod, one end of which carried a cork disk and the other a platinum point by which the circuit was completed. The movement of the medusa against the disk when a stimulus was given, caused the rod to slip upward, thus breaking the chronoscope circuit.

Reaction-Time to Electric Stimuli.

Gonionemus reacts to an electric current, indirectly applied, in from one to five seconds, according to the strength of the stimulus, and the position of the electrodes. The following averages indicate the facts. Since it was not possible to get more than four or five satisfactory reactions in series with any one animal, the averages, unless otherwise marked, are for five reactions.

I. Reactions to a 4-Mesco-cell current, with electrodes on opposite sides of the bell, not in contact with the organism. M. 1.023 sec.; M.V. 0.168 sec.; R.V.[2] 16.0.

II. Same, with 2-cell current. M. 1.489 sec.; M. V. 0.199 sec.; R. V. 13.4.

III. Reactions to a 4-cell current, with electrodes 5 mm. apart in contact with the margin of the bell. M. 0.605 sec.; M. V. 0.128 sec.; R. V. 21.

Repetition of the 4-cell stimulus at intervals of a minute causes

[1] For fuller description of the chronoscopic method used see *Harvard Psychological Studies*, Vol. I., pp. 601–605.

[2] R.V. = (M.V. × 100) / M. = Relative Variability.

a rapid lengthening of the time of reaction. Thus: first reaction, .506 sec.; second, 1.003; third, 3.607.

As compared with the reactions of the small medusa *Gonionemus*, those of the jelly-fish *Cyanea arctica* are slow. Some individual reaction-times of a single individual (*Cyanea*) to a four-cell current, with electrodes in contact with opposite points on the margin follow.

Reaction.	Reaction-Time.	Deviation from Mean.
1	1.026 sec.	.504 sec.
2	1.987	.457
3	1.324	.206
4	1.636	.106
5	1.629	.099
6	1.760	.230
7	1.200	.330
8	1.328	.202
9	1.800	.270
10	1.610	.080
Mean.	1.530	Mean variation. .248

Relative Variability 16.2.

Reaction-Time to Photic Stimuli.

The reaction-time of *Gonionemus* to increase in light intensity, as I have stated in another paper,[1] varies with the strength of the stimulus, temperature, condition of the organism, etc., from one to thirty seconds. To daylight the organism usually responds in about seven seconds; to sunlight the reaction is at first much quicker, but it rapidly lengthens as the organism is exposed to the influence of the intense light. The relation of time of reaction to intensity is indicated by the following averages: Weak daylight, 9.4 sec.; daylight, 7.0 sec.; sunlight, 5.5 sec.

Moreover, the reaction-time varies with the size, sex, and pigmentation of the individual, as well as with such external conditions as temperature, density, and chemical constitution of the medium. Increase in temperature gradually shortens the time from about 8–9 sec. at 19° C., to 2–3 sec. at 32° C. Decrease in temperature lengthens the time, until reactions fail entirely at about 10–12° C.

[1] Yerkes, Robert M., with the assistance of James B. Ayer, Jr.: "A Study of the Reactions and Reaction-Time of the Medusa *Gonionema murbachii* to Photic stimuli." *Amer. Journ. Physiol.*, Vol. 9, 1903, pp. 279–307.

Between these reaction-times of the Cœlenterata and those of most vertebrates, as well as of many invertebrates, there is a striking difference in rapidity. Whereas, the jelly-fish and medusa respond to an electric stimulus in from one to four seconds, the fish or frog responds in a fraction of a second, usually not more than one fourth, and sometimes one tenth. Observe the reaction of the fiddler crab to a shadow, and note how quick it is in comparison with the reaction of *Gonionemus* to the same change in illumination. Is this difference in reaction-time due to a difference in sensitiveness (*i. e.*, is the latency period of stimulation longer); is there a difference in the rate of impulse transmission, of central nerve processes, or of muscle contraction? Such questions should be answered by means of reaction-time investigations. The rate of impulse transmission (presumably nerve transmission) is much slower in the medusa *Gonionemus* than in the vertebrates and most invertebrates thus far studied. Furthermore, it differs for different regions of the medusa; the margin and the radial

Frog.				Medusa.			
Electric Stim. Intensity.	M.	M. V.	R. V.	Light Intensity.	M.	M. V.	R. V.
1	.301 sec.	.085 sec.	28.2	Weak daylight.	9.4 sec.	3.16 sec.	33.6
2	.231 "	.034 "	14.7	Daylight.	7.0 "	2.39 "	34.1
4	.103 "	.012 "	11.6	Sunlight.	5.5 "	1.60 "	29.0

canal regions transmit impulses much more rapidly than do the inter-radial regions. The exumbrellar layer of tissue, so far as I have been able to determine, does not transmit impulses at all.[1]

The frog reacts to such an electric stimulus as was applied to *Gonionemus* in .150–.200 sec. In comparison the medusa's reaction-time is very long; but it differs in yet another respect—it is far more variable. The reaction-times and variabilities of the reactions of frogs to three intensities of electric stimulation as determined in an experimental investigation[2] are here given for comparison with the results given by *Gonionemus* to three intensities of light.

[1] Yerkes, Robert M.: "A Contribution to the Physiology of the Nervous System of the Medusa Gonionema Murbachii. Part II.—The Physiology of the Central Nervous System," *Amer. Jour. Physiol.*, Vol. 7, 1902, p. 193.

[2] *Harvard Psychological Studies*, Vol. I., 1903, pp. 616–618.

This table shows that the relative as well as the absolute variability is higher for the medusa than for the frog. In general it is true that variability increases with increase in the time of reaction. Stimuli or intensities of stimulation which give extremely short reaction-times may be expected to give low indices of variability; similarly animals which are slow in reacting exhibit high degrees of variability. The reflex reaction is absolutely and relatively the least variable among the common types of action; the instinctive reaction is much more variable, and most variable of all in time of execution as also in form, is the voluntary reaction so-called

Relation of Reaction-Time to Region Stimulated.

As might be expected the reaction-time of *Gonionemus* varies with the region stimulated. When the electrodes are placed in contact with the margin at the bases of the radial canals the reaction is noticeably quicker than when the inter-radial regions or other portions of the bell are stimulated. The average reaction-time to a four-cell current applied to the inter-radial portions of the margin is .605 second; for the radial canal regions it is .507 second. It is not necessary, however, to make measurements to thousandths or even hundredths of a second to exhibit this fact; stimulating different regions and simply watching the responses will make clear the differences in reaction-time. Again the time of reaction to light varies according as the light falls upon the subumbrellar or the exumbrellar surfaces. It is much shorter when the subumbrella is exposed to the light (3.4 seconds as compared with 17.4 seconds for the other position).[1]

It is not at all likely that the differences in reaction-time here noted for electric and photic stimuli are due to the same conditions. The quicker reaction to stimulation of the radial canal regions is doubtless due to the higher transmission rate of the differentiated nerve tracts along the radial canals. Stimulation of any other portion of the bell causes reaction less quickly simply because the tissues transmit impulses less rapidly, since they possess less highly specialized nerve tracts. In case of the quicker reaction to light when the medusa is resting with the

[1] *Amer. Jour. Physiol.*, Vol. 9, 1903, p. 301.

subumbrellar, instead of the exumbrellar, surface toward the light, a difference in sensitiveness is apparently the cause of the difference in reaction-time. Certain organs which are especially sensitive to light are found on the subumbrellar surface of the margin, and it is when they are most fully exposed to the action of light that the organism responds most promptly to the stimulus. The rate of impulse transmission is probably the same no matter which surface is stimulated by light, but the latency period of stimulation is far greater for stimulation of the exumbrella.

These experimentally demonstrable facts clearly prove that the nervous system of the medusa *Gonionemus* consists of cells which possess irritability and conductivity in high degrees. And they further show that rapidity of reaction is directly dependent upon specially differentiated paths of conduction.

Reaction-Time of Tentacles.

A study of the reaction-time of the various parts of *Gonionemus* (tentacles, manubrium, margin, bell), when normally functioning, and when isolated by operation, throws interesting light upon certain problems in the physiology of the nervous system.

Cutting off the tentacles close to the bell causes *Gonionemus* a severe shock. If only one tentacle is cut off the usual response is a contraction of the bell, which may occasionally lead to a swimming bout. The severity of the shock, or as we would commonly say, the strength of the stimulus which *Gonionemus* receives from tentacle excision, evidently varies directly with the size of the organ. Small tentacles frequently may be cut without causing any visible reaction except slight contractions of the adjacent tentacles; large tentacles cause one or more contractions, and in general the larger the organ the greater the number and force of the contractions. Excision of the primary tentacles, those at the bases of the radial canals, apparently causes the most severe shock, for when one of them is suddenly clipped off the animal frequently swims about rapidly for a considerable length of time. In every way its reaction is more vigorous than those caused by excision of smaller tentacles or of large tentacles in other positions.

It would appear from this that the radial canal tentacle is of

special significance in the life of the medusa. And in support of this belief it is worth noting that they are almost always held differently from the others. When the majority of the tentacles of a "bell up" (exumbrellar surface uppermost) individual are resting on the bottom of the vessel, the primary tentacles are usually held slightly higher in the water than the others. They are used for attachment and for food seizing sooner than the others. These facts point toward either a specialization or a modification in function which is of interest because of its bearing upon certain neuro-anatomical facts which have been presented by Miss Hyde.[1] She finds well-defined cell-fiber tracts along the radial canals. This being the case we should expect the radial canal tentacles to have a more important and direct influence upon the reactions of the organism than have the other tentacles.

When the medusa is stimulated to motion by light the tentacles contract from .1–.2 second before the bell. At times tentacle reactions occur in the absence of a general bell contraction. As determined with a stop-watch the reaction-time of the normal

I. REACTION-TIME OF NORMAL TENTACLES TO DAYLIGHT.

Tentacle.	M.	M. V.	R. V.
No. 1	2.2 sec.	0.22 sec.	10.0
" 2	3.4 "	0.62 "	18.2
" 3	3.6 "	0.46 "	12.6
General averages.	3.1 —	0.43 +	13.6

II. REACTION-TIME OF TENTACLES OF EXCISED MARGIN TO DAYLIGHT.

Tentacle.	M.	M. V.	R. V.
No. 1	2.5 sec.	0.16 sec.	6.4
" 2	2.7 "	1.06 "	39.2
" 3	2.9 "	0.79 "	27.2
General averages.	2.4 —	0.67 "	24.3

II. REACTION-TIME OF EXCISED TENTACLES TO DAYLIGHT. (AVERAGE OF FIRST THREE REACTIONS.)

Tentacle.	M.	M. V.	R. V.
No. 1	5.3 sec.	2.30 sec.	43.4
" 2	4.2 "	1.92 "	45.2
" 3	4.4 "	1.33 "	30.2
General averages.	4.5 —	1.85 "	39.6

[1] Hyde, Ida H.: "The Nervous System of Gonionema Murbachii," BIOLOGICAL BULLETIN, Vol. IV., 1902, pp. 40–45.

tentacle to the increase in light intensity caused by suddenly uncovering a dish containing the medusa is from two to five seconds. Reaction-time averages for three conditions of the tentacle are given in table on page 90.

A fact significant in this connection is that the excised tentacle rapidly loses its power to react to photic stimuli. To the first four or five repetitions of a stimulus it usually reacts quickly, then the time of reaction, as is shown in the series herewith presented, rapidly increases until reaction fails entirely.

SERIES OF REACTIONS OF AN EXCISED TENTACLE TO DAYLIGHT.

Reaction	1	4.6
"	2	2.5
"	3	8.7
"	4	15.6
"	5	35.0
"	6	No reaction except to
"	7	mechanical stimulation.

The reaction-time of the normal tentacle, 3.1 seconds, is considerably shorter, as would be expected, than that of the bell. Its variability is low. The reactions of the tentacles of excised margins are slightly quicker, 2.4, according to the results presented, than are those of the normal animal, but they are also more variable. The quickness of these reactions may possibly be due to a temporary increase in the irritability of the margin caused by the operation. Finally, the reactions of excised tentacles are much longer, 4.5, and more variable than are those of either the normal animal or the excised margin. This may mean that the tentacle contraction in response to light is normally initiated by stimulation of the margin, or that the ability of the organ to react is lessened by its separation from the bell. At any rate there is a marked difference here indicated in the time of reaction of isolated and normally attached organs, a difference which may possibly be an indication of a function of the central nervous system or of the special organs of light stimulation which are in all probability situated in the margin of the bell.

RELATION OF QUALITY OF STIMULUS TO TIME OF REACTION.

The motor reaction of *Gonionemus* to increase in light is much slower than that to other forms of stimuli. This is due in part

to difference in strength of stimulus, but it is of interest to enquire whether the quality of the stimulus is not of importance. We may ask, for example, whether the reaction-time to the threshold stimulus of all modes of stimulation is the same. If it is not, quality of stimulus is evidently significant. Wundt[1] presents the following figures in support of his statement that the reaction-time to the threshold intensity of all modes of stimulation is the same.

Threshold Stimulus.	Mean.	Mean Variation.
Sound.	.337 sec.	0.50 sec.
Light.	.331	0.57
Touch.	.327	0.32

The results which I have gotten with frogs in working with electric and tactual stimuli cause me to question the applicability of this statement to the reactions of all organisms. It seems highly probable that the just perceptible stimulus reaction-time is by no means the same for different qualities of stimulus. Those modifications of the vital processes which make survival possible appear even in the responses to minimal stimuli. In one case the just perceptible stimulus may cause nothing more than a slight local change in circulation, excretion, muscular action, in another it may produce, just because of the particular significance of the stimulus for the life of the organism, a violent and sudden motor reaction.[2]

Absolute and Relation Variability.

As already pointed out[3] it is generally useless to compare reaction-times with respect to variability unless the reaction-time value as well as the absolute variability is considered. If, for example, to an electric stimulus *Gonionemus* reacts in 2.0 seconds, with a variability of 0.5 sec.; and to a photic stimulus in 6.0 seconds, with a variability of 1.5 sec., it is not correct to say that the reaction-time to light is three times as variable as that to electricity. As a matter of fact the two variabilities as such are

[1] Wundt, Wm.: "Grundzüge der physiologischen Psychologie," Fünfte Auflage, Leipzig, 1903, Dritte Band, S. 428–429.

[2] *Harvard Psychological Studies*, Vol. I., 1903, p. 625.

[3] *Amer. Jour. Physiol.*, Vol. 9, 1903, p. 291.

not equal, but when we consider the reaction-times we find that the ratio of variability to reaction-time is in each case 1 : 4. Although the absolute variability is in one case three times as great as in the other, it is 25 per cent. of the average reaction-time in both instances.

Heretofore I have expressed relative variability as a ratio (M.V. : M.), or as a percentage value of the mean (M.V. = x per cent. of M., in which case x = R.V., the relative variability.)

Obviously it is always important in comparative reaction-time work to know the relative variability of reactions; in fact it is often quite impossible to make significant comparisons of results until this value is found. For this reason I have given in every table of this paper the percentage value of the mean variation in terms of the mean. This value I have called the relative variability (R. V.). It is obtainable by the formula recently used by Myers,[1] v.c. = m.v. × 100/av. In this formula, which as inspection shows gives the ratio (in per cent.) of m.v. to av., v.c. is a value called by Myers the variation-coefficient, and av. is the mean (M.). Supposing a reaction-time of .180 second to have an absolute variability of .020 second, then by the formula (.020 × 100/.180) the variation-coefficient (Myers), or what I prefer to call the relative variability (R. V.), is 11.1 +. If we chose this value might be written 11.1 + per cent., thus indicating that the absolute variability (M. V.) is 11.1 + per cent. of the average reaction-time (M.).

Since Pearson[2] in this statistical work has made use of a quantity which he calls the "coefficient of variability," and which is obtained by the formula

$$\text{C. V.} = \frac{\sqrt{\frac{\Sigma(x^2 \cdot f)}{n}}}{\text{M.}} \times 100,$$

it seems unwise to use the term variation-coefficient, suggested by Myers, for this new quantity in reaction-time work. As the value which we obtain by Myers' formula is in reality the per-

[1] Myers, Chas. S.: "Reports of the Cambridge Anthropological Expedition to Torres Straits." Vol. II., "Physiology and Psychology," Part II., 1903, p. 212.

[2] Pearson, Karl: "Mathematical Contributions to the Theory of Evolution, III., Regression, Heredity and Panmixia," *Phil. Trans. Roy. Soc. London*, Vol. 187, A, pp. 253–318.

centage value of the mean variation in terms of the mean, I see no reason why we should not call it the relative variability, in contrast with the absolute variability. Thus the confusion with Pearson's quantity which will inevitably result from the use of variation-coefficient can be avoided.

Myers' formula gives us precisely what we need for the direct comparison of reaction-times, with respect to their variableness, either to different stimuli or of different organisms. Strange to say most investigators of the time relations of neural processes have paid little or no attention to the variability of their results; none, so far as I know, have ever determined the relative variability throughout their work. It may be objected that those who have use for the relative variability can find it for themselves since the reaction-time and its mean variation are usually given. But the value is far too important to be left half-way determined; in fact it is even more useful in most cases than the mean variation. Every one who has had experience in dealing with reaction-time results will admit that the reaction-time to a particular stimulus has different meanings according to its variability, and that it is never possible to compare reaction-times without considering this value. It is clear then that *no reaction-time statistics should be published without determinations of the relative variabilities.*

Conventionally we compare human reaction-times to visual, tactual and auditory stimuli without noticing their variabilities or the strength of the stimulus employed. Jastrow[1] in a table of results, collected from the papers of many investigators, which is intended to indicate the differences in time of reaction for the different senses gives these averages: Visual reaction-time .185 second; tactile, .148; auditory, .139. Not even the mean variability is given in connection with the averages. Since reaction-time varies with the strength of the stimulus it is possible by varying the stimulus-intensity to get any one of the above reaction-times with any of the qualities of stimulus named. This being true, how are we to make valuable comparisons of reaction-times to different kinds of stimuli?

As before stated the threshold intensities of all modes of stimulation may be regarded as directly comparable. No matter what

[1] Jastrow, Joseph: "The Time Relations of Mental Phenomena," New York, 1890, p. 11.

the form of the stimulus, the threshold gives the longest and most variable reaction-time which can be obtained by the use of that particular quality of stimulus. Now, as the intensity of the stimulus is increased the variability decreases. Why may we not choose equality in relative or in absolute variability as a basis of comparison? If it should be found—and I am now gathering data for the settlement of the point—that the relative variability is the same for the threshold reaction-time to all qualities of stimuli, equality in relative variability would be the most satisfactory basis; if, on the other hand, absolute variability is a constant quantity at the threshold, it should be used in preference.

NOTE.—Reasons have recently appeared for returning to the original spelling of the name of the medusa. *Gonionemus* therefore is used instead of *Gonionema*.